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THE ORIGIN OF *HYPOPTERYGIUM* POPULATIONS IN SOME EUROPEAN BOTANIC GARDENS, WITH SPECIAL REFERENCE TO *HYPOPTERYGIUM ATROTHECA* DIX.

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ABSTRACT

In the second half of the nineteenth century and, in particular, the first decades of the twentieth century many exotic moss species were accidently introduced in European botanic gardens. Several of these introduced mosses have been described as new species. Among them was *Hypopterygium atrotheca* Dix., which grows abundantly in the Glasgow Botanic Gardens.

The present study discusses the "true" origin of *H. atrotheca* and its possible relationships with *Hypopterygium*-species in the wild. *H. atrotheca* was almost certainly carried along with imported tree ferns and shows closest resemblance to Australian material of *H. muelleri*. The introduction of *H. atrotheca* and its "true" origin cannot be fully understood without knowledge of the horticultural history of ferns and the introduction of other *Hypopterygium*-species in European gardens. Hence, the relevant horticultural history of ferns is briefly discussed; the origin of some other, introduced *Hypopterygium*-populations and their relationships with species in the wild are treated as well. Three validly published taxa based on material collected in botanic gardens *(H. atrotheca, H. bouvetti, H. rigidulum spp. balantii)* and a few *nomina nuda* are reduced to *H. muelleri*. *H. immigrans* is also proposed in the synonymy of the latter.

INTRODUCTION

On Monday August 5th, 1996, participants of the British Bryological Society Centenary Symposium, Glasgow, joined a guided tour to the Glasgow Botanic Gardens to see the vascular plants in the Kibble Palace and the Filmy Fern House and, of course, the many bryophytes growing in these greenhouses. Among the mosses was the beautiful *Hypopterygium atrotheca* Dix., which is hitherto only known from these Gardens. *H. atrotheca* is very abundant in the Kibble Palace, where it is found on soil, stones, and bases of trunks of tree ferns, often growing in large, dense groups of mostly medium sized plants. *H. atrotheca* was less abundant in the Tropical Fern House. Only a few plants were found in the Filmy Fern House, but among them were some large ones. Fruiting specimens were, unfortunately, not observed.

H. atrotheca was described by Dixon (1928), who examined fruiting material that was collected by Robert Grierson in the "Kibble Palace Fernery". Dixon reported that "the present species grows, and has been known for more than twelve years, on stems of large tree-ferns and on stones under their shade, where it has spread over a large area". It is most astounding that *H. atrotheca* has now grown and survived in the Gardens for more than 80 years!

H. atrotheca belongs to a small family of pleurocarpous mosses, the Hypopterygiaceae Mitt. They are characterized by having partly or entirely complanate stems and branches, whose complanate parts are set with two rows of asymmetrical, lateral leaves and a single, ventral row of smaller, symmetrical ones (amphigastria). The family contains 7 genera and 24 species. *Hypopterygium Brid.* is the largest genus with 10 species.

The plants of *H. atrotheca* are, like plants of other *Hypopterygium* species, very showy, mostly dendroid and less often pinnate or flabellate mosses. They are differentiated in a creeping rhizome, an ascending stipe, and a frond consisting of a branched rachis and its branches. The plants are variable in habit, the size of the plant, and the degree of ramification. The habit is highly affected by the orientation of the substratum towards the angle of the light.

It is evident that *H. atrotheca* was introduced in the Glasgow Botanic Gardens and originally came from elsewhere. The moss was almost certainly carried along with imported tree ferns. Most of the large tree ferns growing to date in the Kibble Palace originate from Australia, but the "true" origin of the original phorophyte of *H. atrotheca* is not known (cf. Dixon, 1928). It is of botanical interest to know with which *Hypopterygium* species in the wild *H. atrotheca* is most closely related.

Hypopterygium atrotheca: relationships within *Hypopterygium*

The genus *Hypopterygium* occurs in humid, tropical and subtropical regions in both the northern and southern hemisphere, (warm)-temperate regions of the southern hemisphere and eastern Asia, and along the western and north-eastern coast of the Pacific. The mosses are found most abundantly in humid forests, where they grow either terrestrially, on rocks, rotting logs, or epiphytically on tree trunks, branches and on tree ferns. The ecology of *H. atrotheca* in the greenhouses corresponds with that of wild representatives of *Hypopterygium*.

Because of its mostly palmate, less often (bi)pinnate, plants and its entirely tristichous (or nearly so) phyllotaxis, *H. atrotheca* shows most affinity with the *H. tenellum* complex, a group of five very similar and hence probably closely related species. These species occur in South and Central America including the Caribbean (*H. tamarisci* (Sw.) C. Müll.), Africa (*H. laricinum* (Hook.) Brid.), Indo-Malaysian and Sino-Japanese Asia (*H. tenellum* C. Müll.), Melanesia and Polynesia (*H. debile* Reichdt.), and Australia and New Zealand (*H. muelleri* Hampe). In the latter species two groups can be recognized within Australia. A northern group of

monoecious, gemmiferous plants, whose amphigastrium costa reaches usually up to 2/3 of the length of the amphigastrium, predominates in Queensland and New South Wales. A southern group of dioecious, non-gemmiferous plants, whose amphigastrium costa exceeds 2/3 of the length of the amphigastrium, is most frequently found in Victoria, but also occurs in other regions of continental Australia (*H. muelleri* is very rare in Tasmania). Intermediates between these groups are frequently found. Plants of *H. muelleri* from New Zealand resembles most Australian plants of the northern group.

Delimitation of the species within the *H. tenellum* complex is problematic. Morphological differences between the species, which suggest reproductive isolation and support evidence for their status as separate species, are small. *H. tenellum, H. debile,* and *H. muelleri* show such minor differences, that they are possibly conspecific. Identification of material of species belonging to the *H. tenellum* complex without knowing its geographical origin is very difficult.

Unfortunately, the origin of *H. atrotheca* is unknown and hence it was very difficult to ascertain to which wild species of the *H. tenellum* complex *H. atrotheca* has most affinity. In addition, mosses that grow in glasshouses may show poorly developed features or be abnormal. The present study of the origin of *H. atrotheca* was also hampered by the fact that Dixon's type could not be found in his herbarium. It was not in the material of Hypopterygiaceae I had on loan from the British Museum (Natural History) (BM), London, England, and nor did I find it, when I visited this herbarium in 1994. Fortunately, an isotype was present in the material I had on loan from the herbarium of the "Naturhistorisches Museum Wien" (W), Vienna, Austria.

Hypopterygium atrotheca: origin and relationship with *H. muelleri*

H. atrotheca shows closest affinity with *H. muelleri* and it is very similar to plants of this species that come from southeastern Australia. The isotype of *H. atrotheca* is a non-gemmiferous, fruiting plant, which is up to 3.6 cm tall (fig. 1). Its branches are distant or closely set. In a few ramets distant branches predominate resulting in fronds with an open appearance. The costa reaches 2/3 - 3/4 of the length of the lateral leaves and mostly 1/3 - 2/3 of the length of the amphigastria, but is occasionally percurrent in the latter. The amphigastria are short-elliptic to ovate. The isotype is monoecious. Its gametoecia are either unisexual or bisexual, and lack paraphyses. There are up to 7 sporogones per frond. Dixon described the seta as being 1 mm long, which is almost certainly a mistake, and the colour of the theca as dark brownish olivaceous, becoming dark blackish brown when fully ripe. In the isotype, I observed a 7 - 9 mm long seta and an ochraceous theca.

The plants of *H. atrotheca* collected on August 5th 1996, are very similar to the isotype of *H. atrotheca,* especially those from the Filmy Fern House and the Kibble Palace; the plants from the Tropical Fern House are much smaller. Most plants are non-gemmiferous, but a senescing plant possessed gemmaphores. The costa of the lateral leaves and the amphigastria is somewhat longer in the material from the Filmy Fern House and the Kibble Palace and somewhat shorter in that from the Tropical Fern House than in the isotype. The material from the Filmy Fern House and the Tropical Fern House is sterile. The material from the Kibble Palace contains female plants. A non-fruiting specimen of *H. atrotheca* collected by E. Wallace in the Kibble Palace on July 6th 1963, is almost identical to the recently collected material from the Kibble Palace, but is monoecious. Most striking difference between the recently collected, fertile material of *H. atrotheca* and the older material was the presence of a few paraphyses of 5 to 7 cells long in the gametoecia of the former and the absence of such long paraphyses in the gametoecia of the latter. However, the length of the paraphyses in the recently collected material might be abnormal and was possibly induced by the unnatural conditions in the greenhouse. The paraphyses observed in *H. muelleri* and the older material of *H. atrotheca,* if present, are much shorter and hardly distinct from its gametoecial axillary hairs. *H. atrotheca* shows some resemblance with plants of *H. muelleri* of the southern Australian group, but is best considered to belong to the northern Australian group.

Evidence for an Australian origin of *H. atrotheca* was also provided by examination of mosses that grew intermingled with the type material of *H. atrotheca.* Dixon reported that Grierson collected also other mosses in the Kibble Palace Fernery. Among them was an introduced *Achrophyllum*-species, which, according to Dixon, agreed quite well with *Achrophyllum ("Pterygophyllum") dentatum* (Hook. f & Wils.) Vitt & Crosby, which is known from Australia, New Zealand, and southern South America. Dixon suggested that the *Achrophyllum* species might come from New Zealand or South America and he considered it most likely that *H. atrotheca* was imported together with this *Achrophyllum*-species. He remarked, however, that *H. atrotheca* certainly does not agree with any *Hypopterygium*-species from New Zealand.

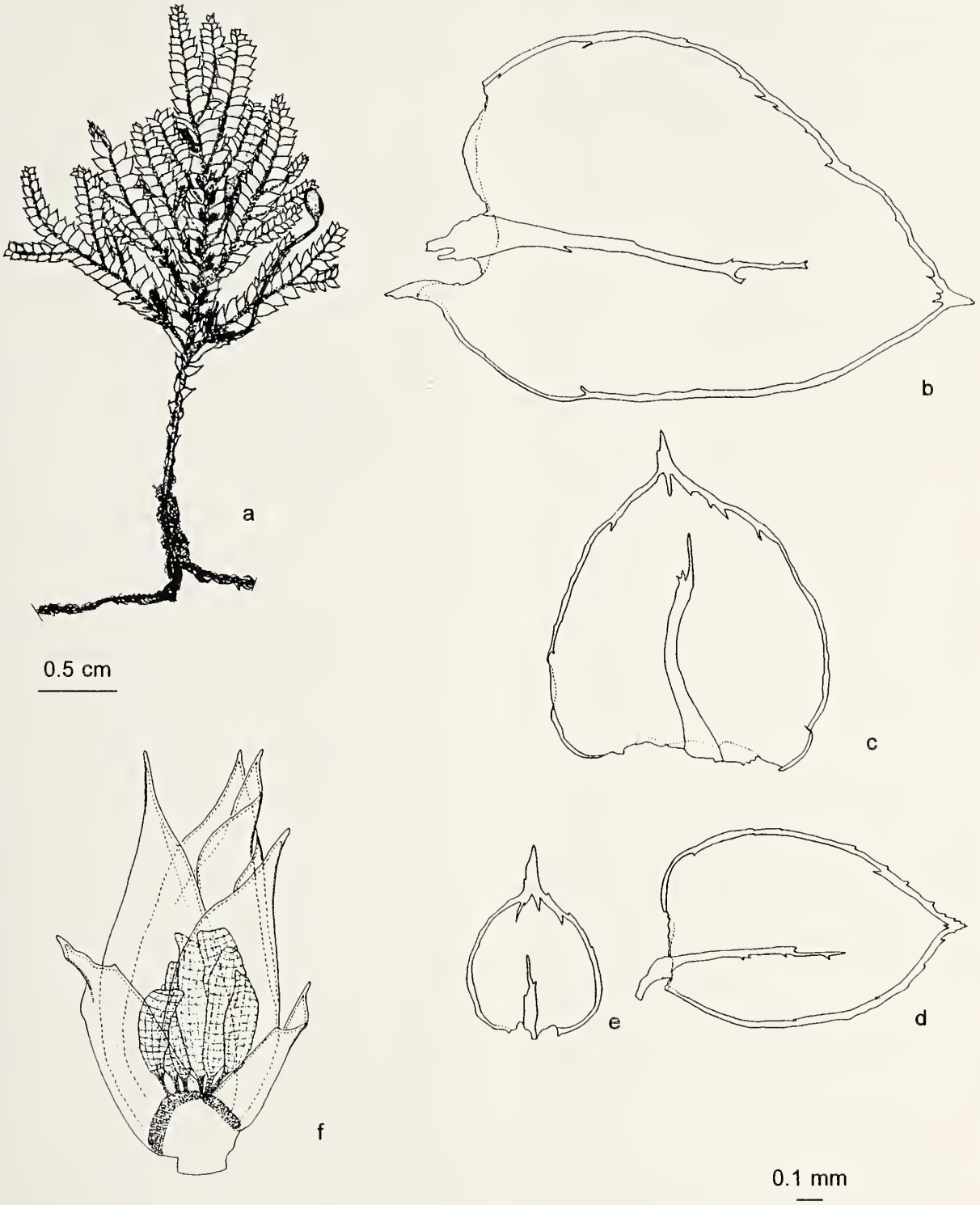
The isotype of *H. atrotheca* is intermingled with a small quantity of *A. dentatum.* If *H. atrotheca* was introduced together with *A. dentatum,* which is very likely, because they were also found growing intermingled on or near tree ferns in greenhouses of other botanic gardens (see below), then *H. tamarisci* may in all probability be discounted as the most closely related species of *H. atrotheca*, because *H. tamarisci* is very rare in southern South America. Thus, the occurrence of *A. dentatum* with the type material of *H. atrotheca* suggests an Australian-New Zealand origin, whereby the material of *A. dentatum* shows closest resemblance to Australian material of this species. Hence, in all probability *H. atrotheca* in the Glasgow Botanic Gardens came originally from Australia, presumably southeastern Australia, and is conspecific with *H. muelleri.*

GENERAL HISTORY

The introduction of *Hypopterygium species* is not unique for the Glasgow Botanic Gardens and has to be seen in the light of the horticultural history of ferns. In the nineteenth century ferns became increasingly popular in Europe, and many tree ferns were imported in the second half of the century, mostly from Australia and New Zealand (cf. Schneider, 1892). The tree ferns were mostly grown in tubs or greenhouses of private owners or botanic gardens, and less frequently outdoors. Epiphytic mosses associated with the tree ferns were frequently carried along and hence introduced.

For instance, the large and, in Australia and New Zealand, well-known moss *Cyathophorum bulbosum* (Hedw.) C. Müll another representative of the Hypopterygiaceae and known

Figure 1. *Hypopterygium atrotheca* Dix. from the Glasgow Botanic Gardens (*Grierson s.n.*). a. habitus; b, c. basal frond leaves; d, e. distal frond leaves (b, d, lateral leaves; c, e amphigastria); f. (male) gametoecium.



from Papua New Guinea, continental eastern Australia, Tasmania, and New Zealand, was collected a few times in greenhouses of the botanic gardens of Charlottenburg, Berlin, (*Graef s.n.*, JE), Munich (*s. coll. s.n.*, JE, 2 specimens), Germany, and Uppsala (*Lindberg s.n.*, S; *Nyman s.n.*, S), Sweden. All specimens collected from these places were found on the trunks of imported *Dicksonia*-tree ferns. The labels of the two collections made in Uppsala indicate that the tree fern comes from New Zealand. The label of one of the two collections made in Munich reports Australia as the origin of the tree fern. Although the origin of the other collections was uninterpretable or not given, they presumably also come from either Australia or New Zealand.

In a similar way *Hypopterygium* species were introduced to European places other than Glasgow. Since 1885, in several botanic gardens, populations of *Hypopterygium* have

been found. Besides *H. atrotheca,* a few of the introduced *Hypopterygia* were described or treated as new species.

Hypopterygium immigrans: origin and relationships

In 1887 Greenwood Pim found a population of *H. immigrans* Lett in his cold fern-house at Easton Lodge, Monkstown, Co. Dublin, Ireland (Lett, 1904). I have seen only a single specimen that is presented as *H. immigrans*, which was collected at the type locality by an unknown collector (TDC). It is a small to medium sized, non-gemmiferous, non-fruiting plant, which, apart from the lack of sporogones, closely resembles Lett's (1904) illustrations of *H. immigrans*.

This specimen is a pinnate, flabellate, to weakly palmate plant, which is up to c. 1.9 cm tall. It is monoecious, having numerous unisexual and few bisexual gametoecia. Most unisexual gametoecia are male. The leaf costa reaches between 1/2 - 4/5 of the length of the leaf. The amphigastria are shortly elliptic to ovate. Their costa reaches at least c. 1/2 of the length of the amphigastrium, and is occasionally faintly excurrent. The frond leaves at the apex of several branches and rachides are absent, which indicates caducous top leaves, which is a common feature in the *H. tenellum* complex.

Lett's (1904) illustrations and the material collected in Pim's fern house show, that Pim's moss almost certainly belongs to the *H. tenellum* complex and shows closest affinity with *H. tenellum* and the northern Australian group of *H. muelleri.* Dixon (1928) remarked that according to Lett's description *H. immigrans* is "a much smaller plant, with more toothed leaves, shorter nerve, and different coloration", but his differences are not substantial. In fact, except for its caducous leaves and monoecy, the material presented as *H. immigrans* resemble small ramets in the type of *H. atrotheca* and the material from the Tropical Fern House in the Glasgow Botanic Gardens.

It was not possible to come with certainty to a more accurate identification of Pim's moss, because its origin is not known. Lett did not give the possible origin of either the moss or its phorophyte, when he suggested that the moss was probably carried along on the roots of a tree fern. However, since most tree ferns that were imported in Europe came from Australia and New Zealand, it is conceivable that Pim's tree ferns originated also from these areas. Supporting evidence for this hypothesis is provided by the fact that it is almost certain that the moss came from a temperate area, because it flourished for at least 17 years in Pim's cold greenhouse (cf. Lett, 1904). This may suggest that *H. immigrans* is conspecific with *H. muelleri.*

Hypopterygium balantii: origin

Presumably between 1893 and 1896, Baenitz distributed, in his exsiccata series *Herbarium europaeum,* specimens of *H. balantii* C. Müll. ex Baenitz, which were collected by P. Sydow between 1891 and 1893 in the "Flora" of the Botanic Garden of Charlottenburg (Berlin, Germany). It is not known with certainty whether this *Hypopterygium* was found growing on a tree fern, but most likely it was.

Between 1884 and 1890 Hugo Graef and other collectors collected material of almost certainly the same moss from in all probability the same trunk of a very old tree fern of *Dicksonia antarctica* Labill. *("Balantium antarcticum")* (cf. Amann, 1913; Warnstorf 1900, 1905). Although the tree fern was first recorded in the seed lists of the botanic garden by Eichler *et al.* in 1878 (the seed lists of 1877 are missing), I did not find such early collections of this moss in all the material that I examined for my forthcoming revision of the Hypopterygiaceae. No specimens were present that with certainty were collected from the tree fern after Sydow's material.

The origin of the phorophytical tree fern of the Charlottenburg mosses is not known. It was not given by, and probably unknown to, the collectors of these mosses. Paris (1896, 1905) suggested New Zealand as the possible origin of the material that was distributed by Baenitz. Warnstorf (1905) reported that his material probably came from Tasmania.

It can be safely assumed, however, that the *Dicksonia antarctica,* and hence the accompaning mosses, came from eastern continental Australia or Tasmania. Schneider (1892) reported that *D. antarctica* was produced in continental Australia, Tasmania, and New Zealand, but it is almost certain that New Zealand as possible origin can be discounted. Schneider, presumably following Hooker f. (1855), included the very closely related *D. fibrosa* Col. (cf. Cheeseman, 1925; Allan, 1961) from New Zealand in his concept of *D. antarctica,* but in the nineteenth century *D. antarctica* was commonly known to come from eastern Australia and Tasmania (e.g. Christ 1897, Hooker & Baker, 1883). In addition, Christ (1897) remarked that *D. antarctica,* from East Australia and Tasmania, was often grown in horticulture.

The *Hypopterygium* from Charlottenburg, like *H. atrotheca* from Glasgow, grew intermingled with *Achrophyllum* Vitt & Crosby. A few collections of the *Hypopterygium* made by Graef and Lucas contain a small quantity of this *Achrophyllum* species. In a posthumous publication, Müller (1902) described the *Achrophyllum* as a new species, *Hepaticina balantii, comb. inval.,* and a small quantity of the *Hypopterygium* was found in, and picked out of, a collection of *Hepaticina balantii* preserved in L. These mosses were collected by Graef in October, 1885, on an old trunk of *Dicksonia ("Balantium"),* presumably the same tree fern from which the other material of *Hypoptrygium* was found. The *Achrophyllum* species was apparently also found on a fern of *Todea barbara* (L.) Moore (Müller, 1902; Warnstorf, 1900, *"Hookeria balantii* C. Müll."), which is known from South Africa, Australia, Tasmania, and New Zealand (Allan, 1961; Field 1890). The fern concerned here was presumably shipped to Europe with the same lot of ferns as the tree fern of *D. antarctica* in Charlottenburg and hence has presumably the same origin, because *T. barbara* was, like *D. antarctica,* first recorded in the seed lists of the botanic garden by Eichler *et al.* in 1878.

In addition, a single collection of *H. balantii* made by Lucas in 1887 (W, *s.n.*) contains a small quantity of *C. bulbosum*, which provides further evidence that the *Hypopterygium* from Charlottenburg came from continental Australia, Tasmania, or New Zealand.

Hypopterygium bouvetii: origin

In 1897 G. Bouvet found a scrap of *Hypopterygium* on an old trunk of *D. antarctica* in a private greenhouse in Angers, Maine-et-Loire, France. Since, he had observed this moss growing on other old trunks of this tree fern-species in greenhouses of the botanical garden of Paris and the horticultural school of Versailles (Bouvet, 1898). As argued above, it is

almost certain that these tree ferns and their accompaning mosses came from eastern continental Australia or Tasmania.

Bouvet (1898) identified the moss as *H. balantii* C. Müll. Although Bouvet's material from Angers is almost identical to small plants found among the material of *Hypopterygium* from Charlottenburg, Bescherelle (1898) described Bouvet's moss as the new species *H. bouvetii.*

Hypopterygium muelleri in Europe

The *Hypopterygia* from Charlottenburg and Maine-et-Loire closely resemble *H. muelleri.* It is beyond any doubt that these "European" mosses are conspecific with *H. muelleri,* because the distribution area of the latter species includes their possible areas of origin. Because *H. muelleri* is rare in Tasmania, it is unlikely that the mosses came from this area.

The *Hypopterygium* from Charlottenburg resembles in many aspects the material from the Glasgow Botanic Gardens. The plants from Charlottenburg are small to medium sized. They are usually flabellate to palmate and loosely or densely branched. Sometimes, the Charlottenburg-material is weakly etiolated and some collections contain a few simple ramets. The *Hypopterygium* from Charlottenburg is obviously monoecious, but female gametoecia may predominate in the collections. Several collections contain fruiting material. Gemmae were rarely found. The leaf costa reaches 1/2 - 3/4 of the length of the lateral leaves. The amphigastrium costa reaches 1/2 - 2/3 of the length of the amphigastrium and is occasionally excurrent. Despite the fact that the costa of the lateral leaves is shorter than usual in *H. muelleri* the *Hypopterygium* from Charlottenburg resembles most the northern Australian group of *H. muelleri.*

The type of *H. bouvetii* is a scanty, non-gemmiferous, sterile plant. Its short stems are simple or loosely branched. The leaf costa reaches c. 4/5 of the length of the leaf. In a few, basal amphigastria the costa reaches c. 2/3 of the length of the amphigastrium, but in most amphigastria the costa is distinctly percurrent. Presumably, *H. bouvetii* has closest resemblance with the southern Australian group of *H. muelleri.*

Warnstorf (in Loeske, 1903) identified a moss that was collected from an old trunk of the tree fern *Cyathea dealbata* (Forst. f.) Sw. in a greenhouse in Wengerode, Germany, as *H. balantii* C. Müll. If this moss was carried along with the tree fern, it may come from New Zealand, the Chatham Islands, or Lord Howe Island (cf. Cheeseman, 1925; Christensen, 1906), but most likely from New Zealand, where *C. dealbata* was collected for horticulture (Schneider, 1892). I have not seen the material that was reported by Loeske, but other material that was collected from the same locality by W Mönkemeijer and Sydow showed that the moss belongs to *H. muelleri.* Mönkemeijer's material, which was collected in 1901, was almost normally developed, whereas Sydow's plant, which was collected 5 years later, is very slender and etiolated.

Such slender and etiolated *Hypopterygia* were also collected by H.N. Dixon in 1908 from a *Dicksonia* in fernhouses of the botanic gardens in Amsterdam, The Netherlands, and, with A.B. Jackson, in Kew, London. According to Dixon's annotations the material from Amsterdam was found together with a *Cyathophorum.* I have not seen the latter moss, but it is almost certain that the *Hypopterygium* belongs to *H. muelleri.* The material from Kew grew in a temperate fern house and is poorly developed, but presumably also belongs to this species.

Dietzow collected a small and somewhat etiolated moss in the Botanic Garden of Königsberg (Kaliningrad), Russia, on *Todea rivularis* Sieb. (= *T. barbara*) in 1933. The fern came from Australia and arrived here in about 1903. There is little doubt that Dietzow's moss belongs to *H. muelleri.*

A few other *Hypopterygia* found in greenhouses of European botanic gardens presumably also belong to *H. muelleri.*

In 1903 Amann (1913) collected *H. balantii* C. Müll. ex Baenitz at the base of a trunk of *D. antarctica* in the "Palais d'hiver" of the "Jardin d'Acclimatation", Paris, France. Presumably, this moss had earlier been noticed by Bouvet (1898). Amann collected a good quantity of the moss, which is well developed and closely resembles small, terrestrial plants of *H. muelleri.* It is almost certain that this moss came originally from continental Australia or Tasmania.

In 1910 Gustav Schellenberg found *H. balantii* on tuff stones in the palm house of the botanical garden of Zurich, Switzerland. This male plant, which is occasionally gemmiferous at damaged stem parts, resembles the material of *H. atrotheca* from the Glasgow Botanic Gardens, but is more slender and partly somewhat etiolated. Its identity is not known with certainty, because its origin is completely unknown. This is also the case for a collection made by C. Cool in 1926 in the Botanic Garden of Leyden, The Netherlands, and a collection made by R.A.L. Potier de la Varde in the Palmarium of the Botanic Garden of Caen, France. Cool's moss is slender and partly gemmiferous and shows a strong resemblance with a few ramets in Schellenberg's collection that have closely set branches. Potier de la Varde's moss is etoliated and resembles the material from Wernigerode and Amsterdam.

The only locality known in Europe where *H. muelleri* grows outdoors is the Bussaco Forest in Portugal. The Bussaco Forest is an arboretum where since the nineteenth century exotic tree species have been introduced (V. Allorge, 1974). In this arboretum the moss is only found in the proximity of a cascade ("Cascata"), where it was found at first in 1929 by P. and V. Allorge (cf. Anonymous, 1931). The moss is still present in the Bussaco Forest and maintained here for more than 67 years. According to Cecília Sérgio (in litt., 1996) the population of *H. muelleri* is very large and even seems to be extending.

It is beyond any doubt that the moss is accidently introduced in Portugal. It is not known when *H. muelleri* arrived here (cf. V. Allorge, 1974), but presumably in or after 1887, when the cascade in the Bussaco Forest was constructed (V. Allorge, 1974). In 1931 P. Allorge sent material of *H. muelleri* to H.N. Dixon and wrote that he thought that the moss was introduced with exotic trees or with tree ferns, like in many greenhouses. According to V. Allorge the cascade is overshadowed by exotic trees, shrubs, and tree ferns. Seen in the light of the preceding, in all probability the moss was accidently transported with one of these tree ferns.

The Portuguese material shows a close resemblance with terrestrial plants of *H. tenellum* and *H. muelleri,* but shows its closest resemblance with terrestrial plants of the latter species from southern New South Wales and Victoria, Australia. The Portuguese material is intermediate between the two Australian forms of *H. muelleri.*

Other *Hypopterygium*-species

The *Hypopterygium* that has been grown on lava boulders in the hot houses of the Botanic Gardens of Utrecht, The Netherlands, since 1967 belongs to the *H. tenellum* complex, but its precise identity is not known. It shows no decisive morphological features and its origin is unknown.

In 1903, a few days after he collected *H. balantii* C. Müll. ex Baentiz on a trunk of *D. antarctica* (see above), Amann (1913) found a small quantity of this moss on *D. sellowiana* Hook in the hothouse of the "Jardin des Plantes" in Paris. It is almost certain that Amann did not collect the moss from the *D. sellowiana*, a tree fern known from southern Brazil, and its identity remains uncertain. Presumably, this moss belongs to *H. tamarisci,* although dispersal of the moss found on the *D. antarctica,* which belongs to *H. muelleri,* cannot be ruled out.

Not every introduced *Hypopterygium* belongs to the *H. tenellum* complex. Recently, E. Urmi found etiolated material of *H. vriesei* Bosch et Lac., known from Indo-malaysia, in the new Botanic Gardens of Zurich. This material is distinctly gemmiferous with numerous green, filiform gemmae that are situated in bundles in the axils of mainly the lateral leaves. Once, a specimen of *H. didictyon*, known from southeastern Australia, New Zealand, and southern South America, was found by Rev. Eloc on a tree fern of *D. antarctica* in a greenhouse in Neuilly near Paris. In nature, *H. didicyton* is much less often found on tree ferns than *H. muelleri.*

However, despite the latter findings, as a result of the importation of tree ferns in majority from Australia and New Zealand, where *H. muelleri* is the *Hypopterygium* species which is most frequently found growing on tree ferns, most of the *Hypopterygia* that were introduced in Europe between 1875 and 1930, including *H. atrotheca,* belong to *H. muelleri.*

NOMENCLATURE

In the course of this study, *Hypopterygium atrotheca* and *H. bouvetti* were considered to be conspecific with *H. muelleri* and are synonymized below. *H. immigrans* is proposed in the synonymy of *H. muelleri.*

The nomenclature of the names based on the *Hypopterygium* from Charlottenburg is problematic. Notes on these problems follow. It is evident that the *Hypopterygium* from Charlottenburg is conspecific with *H. muelleri.* Hence, the names attached to the *Hypopterygium* from Charlottenburg are synonymized with *H. muelleri* below.

Nomina nuda

Baenitz, in his exsiccata series, and Warnstorf (1900) treated *H. balantii* as a known species, which they ascribed to Müller. However, although Müller (1902) described the *Achrophyllum* species that was found in Charlottenburg, he did not publish on *H. balantii.* Neither Baenitz nor Warnstorf provided *H. balantii* with a description. Paris (1896, 1905) and Amann (1913) are the only authors who referred to Müller's name in Baenitz' exsiccata series, but they did not provide it with a description either.

It is not known whether Müller actually identified Sydow's material in Baenitz' exsiccata series. Baentiz did not indicate this material as belonging to a new species. Only specimens collected by Graef (and Graef & Lucas) on 13 November, 1885, and November, 1888, were presented as such.

Warnstorf (in Loeske, 1903) identified the material from Wernigerode as *H. balantii.* The name *H. balantii* was also used by Warnstorf in 1905, but neither Warnstorf (1905) nor Loeske (1903) provided *H. balantii* with a description. They neither referred to the only validly published taxon that was based on the Charlottenburg material: *H. rigidulum* Mitt. spp. *balantii* C. Müll. ex Kindb., a subspecies described by Kindberg (1901).

Wijk et al. (1964: 178), erroneously ascribed H. balantii C. Müll. to Loeske (1903: 333), and overlooked not only Müller's name in Baenitz' *Herbarium europaeum,* but also the other names published before 1903: Paris (1896: 699), and Warnstorf (1900: 66). Presumably they also overlooked the names given by Paris (1905) and Amann (1913).

Hypopterygium muelleri Hampe

Linnaea 28: 215 (1856). - *Pterobryon muelleri* (Hampe) Mitt., Trans. Roy. Soc. Victoria 19: 81 (1882). - Type: Australia, Victoria: *Austr. felix., In lapidibus ad ripam fluminis Buchan humidam ("Ad ripas flum. Buchan-river"*), March, 1854, *von Mueller s.n.* (BM holo, not found; MEL holo?, sub no. **40**; MEL iso, sub no.'s **40** and **111**).

Types of *H. muelleri* Hampe are absent from Hampe's herbarium kept in BM and were not found in other herbaria, except for two specimens in MEL. The potential holotype is provided with annotations by Hampe.

Hypopterygium bouvetii Besch., Bull. Soc. bot. Fr. 45: 490. 1898, *syn. nov.* - Type: France, Maine-et-Loire, Angers, sur les troncs de fougères arborescente dans les serres de M. Fargeton ["dans les serres des établissements horticoles, sur vieux stipes de *Balantium antarcticum*"], July 29, 1897, *Bouvet s.n.* (BM holo not found, PC!, mixed with *Racopilum* spec.).

Hypopterygium rigidulum Mitt. ssp. *balantii* C. Müll. ex Kindb., Hedwigia 40: 295. 1901, *syn. nov.* - Syntypes: Germany, Berlin, Charlottenburg, Botanic Garden of Berlin: palm house of the "Flora", "ad trancum *Balantii antarctii",* Nov. 13, 1885, *Graef s.n.* (B destroyed; S lecto!, sub. no's 45 and 33 in hb. Kindberg; JE!); "ad truncum [putrid.?] *Balantii antarctii",* Nov. 1888, *Graef s.n.* (B. destroyed; S!, sub. no's 45 and 33 in hb. Kindberg, JE!). - Lectotype selected here.

The specimen collected by Graef in 1888 is preserved in Möller's herbarium kept in S. Although there is no direct evidence that Kindberg saw this material, it is almost certain that he examined it for his revision (1901).

?Hypopterygium immigrans Lett, J. Bot., Lond. 42: 249, t. 463. 1904, *syn nov.* - Type: Ireland, Co. Dublin, Monkstown, Easton Lodge, ["On surface of earth in pots and rock-work in cold fernhouse"], 1887, *Pim s.n.* (not found).

The only specimen presented as *H. immigrans* that I have seen is presented as an isotype of *H. immigrans,* but there is no evidence for this. The specimen was collected by an unknown collector at the type locality of *H. immigrans* and it is preserved in TDC. It is not clear whether the specimen was collected in 1904 or had been collected earlier and was sent to Lett (or any other person) in that year. The specimen is a non-fruiting plant. Lett (1904), on the other hand, described fruiting material.

Hypopterygium atrotheca Dix., J. Bot., Lond. 66: 350. 1928, *syn. nov.* - Type: United Kingdom, Scotland, Glasgow, Botanical Gardens, Kibble Palace Fernery, tree ferns, "Origin

unknown. But *soc. cum Pterygophyllo dentato"*, Febr. 1927, *Grierson s.n.* (BM holo not found, W!).

Hypopterygium balantii C. Müll. ex Baentiz, *Herbarium europaeum,* series number not known, collection no. **8088**, "Flora Marchica, 1891 - 93"; exsiccata presumably distributed between 1893 and in or before 1896, *nom. nud., syn. nov.* - *Hypopterygium banlatii* C. Müll. ex Amann, Revue. bryol. 40: 24. 1913, *typograph. err. pro* [*Hypopterygium balantii* C. Müll. ex Baenitz]. - Original material: Germany, Berlin, Charlottenburg, "Flora", *Sydow s.n.* (B destroyed; JE!, L!, S!, Z!).

Baenitz' *Herbarium europaeum* is an exsiccata series that contains mainly phanerogams, but also few cryptogams, including mosses. The label of the original material of *H. balantii* C. Müll. ex Baenitz was neither provided with a series number of the *Herbarium europaeum*, nor with date or year of distribution. These data could not be traced. A collection number was given for only a single specimen (in S). Purchasers of Baenitz' exsiccata and those interested in his *Herbarium europaeum* could order catalogues from Baenitz. Such catalogues were not found. They were presumably cut to labels for the obtained specimens. If so, the labels of specimens examined are identical with the text of Baenitz' catalogue that is of concern here. These labels are not provided with a description or diagnosis.

Hypopterygium balantii C. Müll. ex Bouvet, Bull. Soc. Étude. scient. Angers 27: 138. 1898, *nom. nud., syn. nov.;* presumably based on *Hypopterygium balantii* C. Müll. ex Baenitz.

Hypopterygium balantii C. Müll. ex Warnst., Verh. bot. Ver. Prov. Brandenb. 41: 66. 1900, *nom. nud.;* C. Müll. ex Warnst. in Loeske, Moosflora des Harzes: 333. 1903, *nom. nud.;* C. Müll. ex Warnst., Kryptogamenflora Mark Brandenburg: 659. 1905, *nom. nud.; syn. nov.* - Original material: Germany, Berlin, Charlottenburg, Botanic Garden of Berlin: palm garden "Flora", "ad truncum *Balantii antarctii"*, Nov. 13, 1885, *Graef s.n.* (B destroyed; S lecto!, sub. no's 45 and 33 in hb. Kindberg, JE!).

The original material is also a syntype of *H. rigidulum* Mitt. ssp. *balantii* C. Müll. ex Kindb.

Specimens of *Hypopterygium* examined

Angers: *Bouvet s.n.* (1897; PC). Amsterdam: *Dixon s.n.* (1908; BM). Bussaco: *P. & V. Allorge, Bryoth. Iber. 146* (1929; L, S, ZT; BM, *s.n.*), *Florin s.n.* (1930; S), *Rozeira s.n.* (1936; S), *Sérgio 2259* (1979, L). Caen: *Potier de la Varde s.n.* (1930; BM) Charlottenburg: *Graef s.n.* (22 Oct., 1884; Z), *s.n.* (12 Oct., 1885; JE), *s.n.* (13 Oct., 1885; S), *s.n.* (14 Oct., 1885; L, picked out a collection of *Hepaticina balantii*); *s.n.* (13 Nov. 1885; JE, JE *p.p.*, S *p.p.*, sub no.'s **45** and **33**), *s.n.* (1888; JE, S, sub no.'s **45** and **33**), *s.n.* (1889; JE), *s.n.* (without date; L); *Graef & Lucas s.n.* (13 Nov., 1885; S); *Hennings* (**44** + **36**) (without date; S, received in 1900); *Lucas s.n.* (1887; JE *p.p.*, W *p.p.*), *s.n.* (1888; GRO, JE), *s.n.* (1890, S, ZT), *s.n.* (without date; JE), *Sydow, "Flora Marchica, 1891 -93" s.n.* (1891 - 93; JE, L, S, Z). Glasgow: *Grierson s.n.* (1927; W), *Kruijer 96.08.01a-c* (1996, L), *Wallace s.n.* (1963, Z). Kew: *Jackson & Dixon s.n.* (1908; BM). Kaliningrad (Königsberg): *Dietzow s.n.* (1933; BM). Leyden: *Cool (3169)* (1926; GRO). Monktown: *s. coll., s.n.* (1887; TDC). Neuilly: *Eloc s.n.* (without date; S). Paris: *Amann s.n.* (1903; Z). Utrecht: *Kreulen s.n.* (1967; GRO), *Aptroot & Kruijer 90.03.01* (1990; L). Wernigerode: *Monkemeijer s.n.* (1901; JE), *Sydow s.n.* (1906; S). Zurich: *Schellenberg s.n.* (1910; S, Z), *Urmi s.n.* (1996; Z).

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